

A lifetime perspective of biomass allocation in *Quercus pubescens* trees in a dry, alpine valley

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Abstract Plasticity of biomass allocation is a key to growth and survival of trees exposed to variable levels of stress in their lifetime. Most of our understanding of dynamic biomass allocation comes from seedling studies, but plasticity may be different in mature trees. We used stem analysis to reconstruct whole-tree growth and biomass allocation patterns in *Quercus pubescens* trees harvested from a dry woodland in Valais, Switzerland. We identified three distinct growth phases. In phase I, a primary root developed but the aboveground structure did not persist. In phase II, height growth occurred and secondary roots developed. In phase III, height growth ceased and stems and roots only grew radially. Reference trees harvested from a less dry site nearby only showed phase II-type growth. In line with our hypothesis, drought-stressed trees maintained more biomass in roots and less in aboveground woody parts than reference trees. Contrary to our expectation, stressed trees allocated proportionally more

resources to leaves and less to roots in the growing season before harvest than reference trees. It appears that sub-seasonal wood anatomical adjustments to water availability minimize hydraulic failure, thus enabling these dry woodland trees to invest preferentially in leaves. Wet years did not see preferential investment in aboveground tissues, suggesting more restricted plasticity in biomass allocation in these mature trees than in seedlings. It is concluded that trees beyond seedling stage show different responses to variation in drought than the better-studied seedlings.

Keywords Biomass distribution · Dry woodland · Root/shoot ratio · Stem analysis · Water relations

Introduction

Plasticity of biomass allocation in response to environmental stress contributes strongly to the success of plants and is, in fact, thought to be more important than plasticity in physiological traits (Weiner 2004). Plastic responses of biomass allocation to biotic and abiotic conditions enable plants to maintain functional relationships among leaves, stem and roots (Cannell and Dewar 1994; McConnaughay and Coleman 1999; Martinez-Vilalta et al. 2007). In dry woodlands, an important question is how plants allocate biomass among fine roots for water and nutrient acquisition; coarse roots, stem and branches for water transport; and leaves for transpiration and light capture.

Following the functional equilibrium hypothesis (Brouwer 1962), plants in dry conditions are expected to invest proportionally large amounts of biomass in water acquisition and transport structures. Such high investment in roots and aboveground woody tissue prevents the occurrence of harmfully low water potentials in plant tissues

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(Martinez-Vilalta et al. 2007), reduces the risk of cavitation in the xylem (Zweifel and Zeugin 2008; Galle et al. 2010), and postpones stomatal closure (Tyree and Zimmermann 2002). Plants in dry environments thus trade off high investment in water acquisition and transport against investments in leaves, leading to reduced light capture and subsequently lower growth rates (Weber et al. 2007). Given this trade-off, relief from drought stress should allow for increased investment in leaf display and light harvesting.

Our understanding of biomass allocation in response to environmental stress is primarily based on seedling studies (e.g., McConnaughay and Coleman 1999; Sack and Grubb 2002; Markesteijn and Poorter 2009). However, mature trees may behave differently than seedlings. For example, larger trees can store more reserves than seedlings (Chapin et al. 1990) and may thus not need to change biomass allocation patterns to survive episodic stress. Moreover, the capacity to acclimate to (periodic) stress conditions might be lower than that of seedlings (Niinemets 2010). Finally, in mature trees the costs of maintaining high plasticity may outweigh the benefits (DeWitt et al. 1998).

How to measure lifetime growth and biomass allocation patterns of mature trees? Stem analysis, a technique of examining the growth rings of sections from a tree trunk, is a powerful tool that can provide information on cumulative wood production within the whole woody plant (Fayle 1975; Drexhage et al. 1999). Annual increment of woody tissues can also be reconstructed and linked to environmental data. Here, stem analysis, extended to include coarse roots, is used to reconstruct whole-tree biomass allocation patterns in pubescent oak trees (*Quercus pubescens* Willd.) harvested from a dry woodland in the central Rhône valley (Valais) in Switzerland (hereafter referred to as ‘stressed trees’). We contrasted these ‘stressed trees’ with individuals harvested from a nearby site that is less dry (‘reference trees’).

Following the functional equilibrium hypothesis, we expected that stressed trees (1) maintain proportionally more root biomass and less aboveground woody biomass than reference trees; (2) allocate more biomass to aboveground wood and less to leaves than reference trees and (3) preferentially invest in aboveground structures in years with high precipitation. To test these hypotheses we analyzed diameter increment and longitudinal growth of stems and roots and linked these data with growing season precipitation data collected at a nearby weather station.

Materials and methods

Study site

The study was carried out at two sites (Salgesch and Jeizinen) with contrasting conditions in Valais, Switzerland,

an inner-alpine valley with cold winters and warm summers, and an annual precipitation of ca. 600 mm (Table S1). Summer months are characterized by moisture deficit, with potential evapotranspiration exceeding precipitation (Weber et al. 2007).

The stressed trees grew on a south-exposed slope near Salgesch (46°19′27N, 7°34′40E) at 975 m a.s.l. The soil at this site is 10–30 cm deep and classified as a rendzic leptosol on solid rock limestone (Rigling et al. 2002). This type of soil has low water-holding capacity. The reference trees grew near Jeizinen (46°19′40N, 7°34′40E) at 1,270 m a.s.l. in deeper soil (50–130 cm) with better water-holding capacity. This site has lower vapor pressure deficit and less negative soil water potential (Zweifel et al. 2006, 2009). *Quercus pubescens* (pubescent oak) is at both sites co-dominant with Scots pine (*Pinus sylvestris* L.). Mature oaks are 2–5 m tall at the dry site, and 4–12 m at the reference site and crown cover is lower at Salgesch. Pictures illustrating the physiognomy of the two sites can be found in Fig. 2 of Zweifel et al. (2009).

Because biomass allocation is more dependent on size than on age (Coleman et al. 1994; Weiner 2004; Martinez-Vilalta et al. 2007), we compared stressed trees with reference trees of similar size. Climate data were obtained from the nearby national meteorological station of Sion (MeteoSwiss: 46°13′11N, 7°19′36E; Table S1). Total precipitation from March to June was used to test the correlation of precipitation with ring width series, because these months are most influential for radial growth of *Q. pubescens* in this area (Zweifel et al. 2006).

Tree sampling

At the end of the 2004 growing season, eight oaks of 2–4 m height were harvested, four at the dry site and four at the reference site. Due to the relative inaccessibility of the site, neither hydraulic nor air-jet excavation was possible, so we carefully excavated all roots >0.5 cm in diameter by hand for two trees per site, manual root excavation of adult trees in rocky soil being too labor intensive to complete for all trees. From every branch of these four trees a disc was taken at 10 cm radial distance from the stem. The stem was cut in segments and at every 50 cm a disc was taken. The primary root was cut in slices of 2–5 cm thick. Discs from the secondary roots were taken at every 20 or 50 cm, depending on the diameter variation. Disc circumference and length were determined to calculate wood volume. The four trees from which we could not extract roots were used for analysis of height growth and aboveground biomass allocation only. For each tree all leaves were oven dried at 70 °C for >96 h and total leaf dry mass was determined.

Tree ring measurements

Surfaces of all discs were polished (up to sandpaper grit 800), or prepared with a razor blade to make ring boundaries clearly visible. Ring numbers were counted on all discs. Ring widths were measured for discs from stems and primary roots using a binocular microscope, and were recorded in TSAP-Win (Rinn 2003) and plotted as time series. To trace partly missing rings and to cross-date ring width series, we first derived reference ring width series for the eight oaks from the samples taken at the stem base. Discs from the primary root were measured using these reference series and, one by one, lower discs were cross-dated. Rings of secondary root discs were only counted, as the increasingly diffuse-porous structure and vague ring boundaries, common for deeper roots (Drexhage et al. 1999; Gärtner 2007), made accurate quantification of ring width impossible.

Volume and biomass calculations

To estimate volume and mass the 50-cm stem segments were considered truncated cones, and the top segment a full cone. Stem mass was calculated as:

$$\text{Stem mass (g)} = (0.79) \times \left[\sum_{i=1}^{n-1} \left(\frac{1}{3} \cdot \pi \cdot h \cdot (r_l^2 + r_l \cdot r_u + r_u^2) \right) + \left(\frac{1}{3} \cdot \pi \cdot h \cdot r_l^2 \right) \right]$$

where 0.79 is the average wood density of *Q. pubescens* trees at this site [determined with the water replacement method for bark-free stem discs taken at 1 m height from ten trees (Sterck et al., unpublished data)]; n is the number of stem segments, including the top segment; h is the height of the segment in cm; and r_l and r_u are the radii in cm of the lower and upper cross sections of the segments, respectively. Wood density of 0.79 g/cm³ is in the high range of values published for this species, but not uncommon for trees growing under dry conditions high on hill slopes (Barij et al. 2007).

To estimate biomass investment in root, stem, and branches in the growing season before the trees were harvested (2004), the estimated volume of wood that had accumulated until 2003 was subtracted from the estimated volume of wood at harvest, and mass was calculated from wood volume as above. Branches were not divided in segments, so the 2004 biomass investment in branches was calculated as: [(year ring area₂₀₀₄)/(total cross-section area)] × (branch mass) and then summed across all branches.

Statistical analyses

Parameters of stressed and reference trees were compared using Wilcoxon rank-sum tests. Correlations between stem

and root ring width chronologies, and between ring width and precipitation, were analyzed with Spearman's rho. Analyses were performed in R version 2.6.0 (R Development Core Team 2007) or JMP 8 (SAS Institute, Cary, NC, USA).

Results and discussion

Tree status

Stressed trees were older, had a larger diameter at breast height, and had higher total biomass than reference trees at comparable tree height (Table 1). The major portion of the below-ground biomass was located immediately below the trunk base, as previously described in Di Iorio et al. (2005). Primary roots of stressed trees were not only thicker than the stem just above the soil surface; they were also older (Table 1). These older primary roots supported greater biomass of secondary roots than primary roots of reference trees did (Fig. 1). Thus, in line with hypothesis 1, drought-stressed trees maintained proportionally more biomass in roots and less in stems and branches than reference trees (Fig. 1). This finding supports the functional equilibrium hypothesis and suggests that in water-limited conditions proportionally more resources must be invested in roots to maintain a given aboveground biomass (Litton et al. 2007).

Interestingly, in contradiction with hypothesis 2, in the very dry 2004 growing season stressed trees allocated a much larger proportion of aboveground biomass to leaves, and a smaller proportion to wood than reference trees ($P < 0.05$; Fig. 1b). Ring width and growing season precipitation were significantly correlated for both stems and roots of stressed trees (all $P < 0.1$), but not for reference trees. Furthermore, a strong correlation existed between annual diameter growth of stems and roots ($P < 0.05$; Fig. 2). These correlations suggest that in contrast to hypothesis 3, years with relatively high precipitation did not see preferential biomass investment in aboveground structures.

In the following, we will first describe the detected growth patterns and then discuss those results in light of our central hypotheses.

Growth history

We distinguished three growth phases for the stressed trees (Fig. 3a, b). In phase I (ca. 25 years), aboveground structures did not persist, suggesting that the shoots died back, possibly repeatedly, between 1935 and 1960. This may have occurred as a result of biotic disturbances, such as browsing by goats or stem harvest for viniculture (Gimmi and Bürgi 2007; Gimmi et al. 2010). Consequently, the

Table 1 Overview of height, age, diameter at breast height (DBH) and biomass of stressed and reference (Ref.) *Q. pubescens* trees harvested from the Valais, Switzerland

Tree	Site	Age (year)		DBH (cm)	Height (m)	Biomass (kg)					Biomass investment 2004 (g)				
		$H_{-0.10}$	$H_{0.0}$			Root	Stem	Branch	Leaf ^b	Total	Root	Stem	Branch	Leaf ^b	Total
S1	Dry	67	51	6.4	3.6 ^a	12	12	3.3	1.2	28.5	73	274	289	1,875	2,511
S2	Dry	71	42	4.5	2.9 ^a	7	6	1.7	0.4	15.1	17	62	62	418	559
S3	Dry		42	3.9	2.7 ^a		4	2.8 ^b	0.4			65		445	
S4	Dry		53	2.7	2.5 ^a		3	1.2 ^b	0.3			22		257	
R1	Ref.	18	15	1.4	2.9	1	2	0.8	0.4	4.2	101	279	151	441	972
R2	Ref.	14	13	3.5	3.4	3	2	1.7	1.2	7.9	244	433	376	1,166	2,219
R3	Ref.		15	2.3	2.3		2	2.2 ^b	0.5			101		450	
R4	Ref.		13	2.4	3.9		4	2.3 ^b	1.2			444		1,169	

$H_{-0.10}$, $H_{0.0}$ height of the discs in the tree, respectively at 0.10 m below, and at the soil surface

^a Height from soil surface to highest branch

^b Weighed values (not calculated)

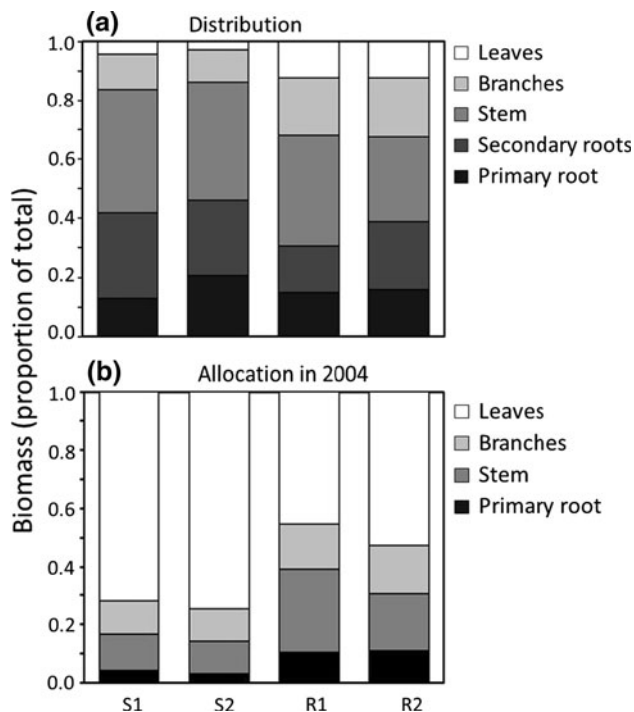


Fig. 1 Proportional distribution of biomass (a) and allocation to leaves, branches, stem, and roots in the 2004 growing season (b) of two drought-stressed *Q. pubescens* trees (S1, S2) and two reference trees (R1, R2). Secondary roots are only included in the biomass distribution graph, as ring width could not be determined on discs from secondary roots

primary roots were older than the stems just above the surface (Table 1). Other oak species have also been shown to have older roots than stems when grown in harsh environments (Johnson et al. 2002), highlighting the capacity of this genus to withstand harsh conditions by re-sprouting following stem dieback. Dieback may also have been caused by frost or summer drought, both of which

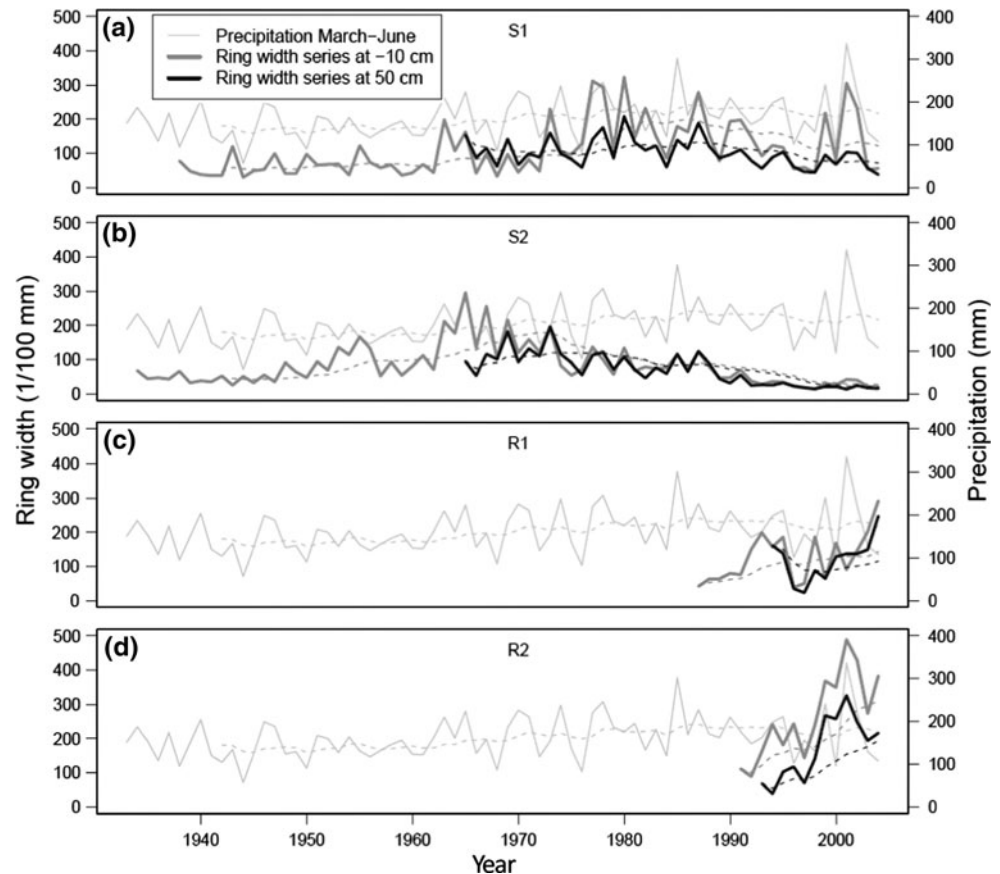
commonly occur in the area. Because browsing, stem harvesting, drought, and frost can all cause dieback of stems, we cannot make inferences about the causes of aboveground dieback in phase I, and only note the effect, namely, buildup of below-ground biomass, rich in reserves.

Phase II lasted another 25 years (~1960 to 1985). In this period trees grew in height and produced almost all the secondary roots that persisted until tree harvest in 2004 (Fig. 3a, b). The height growth rate of $10 (\pm 3)$ cm per year (mean ± 1 SD) during this phase was significantly lower than height growth rate in reference trees (23 ± 3 cm) (Wilcoxon rank-sum test for comparison of the slopes of the linear part of the phase II height growth curves of all eight trees ($P < 0.05$; Fig. 3c, d). The decline in goat numbers and stem harvest in Valais between 1950 and 1970 (Rigling et al. 2006; Gimmi and Bürgi 2007) could explain why the stressed oaks produced a persistent stem only from 1960 onward.

In phase III net height growth and production of persisting secondary roots ceased. The stressed trees did not get taller than 3–4 m, most likely a result of hydraulic limitation (Ryan et al. 2006), as suggested by earlier studies of *Q. pubescens* in Valais (Weber et al. 2007; Zweifel et al. 2007). Reference trees only had phase II-type growth (Fig. 3).

These height growth patterns were strongly associated with the dynamics of radial growth of stems and roots. In phase I, radial growth of the primary roots was comparatively stable (Fig. 3). Ring widths of primary roots peaked in phase II and then gradually declined again in phase III. Most secondary roots developed in phase II. Coutts and Nicoll (1991) found that taproot growth generally slows down as growth of secondary roots increases. In the drought-stressed trees in our study this was clearly not the case (Fig. 3). The aboveground development in phase II

Fig. 2 Ring width of stems (**bold black line**) and roots (**bold grey line**) (*left axis*) plotted as time series. *Solid lines* represent annual variations; *dashed lines* represent the 10-year moving averages. On the secondary y-axis the precipitation between March and June for each year (*solid grey line*) and its 10-year moving average (*dashed grey line*) are plotted



and the maintenance of a canopy presumably generated sufficient energy for extensive secondary roots to develop; at the same time the primary root was probably used for carbohydrate storage (e.g., Barbaroux et al. 2003). Hydraulic limitation may have prevented further height growth at any given year and investment in below-ground storage would thus have been beneficial (Bloom et al. 1985; Chapin et al. 1990).

Interestingly, radial growth of the primary root in phases II and III was strongly correlated with the radial growth of the stem for all trees (all $P < 0.01$; Fig. 2). Correlations between radial growth of roots and stems were also found for other temperate tree species that were harvested from more mesic woodlands, including several oak species (Krause and Eckstein 1993; Drexhage et al. 1999). The correlations between radial growth of both stems and roots of stressed trees and growing season precipitation were strong when analyzed for the period of active height growth (phase II in Fig. 3) ($P < 0.05$), but weaker ($P < 0.1$) when calculated over the whole period of aboveground growth (phases II and III). For reference trees ring width did not correlate with growing season precipitation, supporting the notion that growth was indeed not as limited by water availability as at the dry site (Zweifel et al. 2009). The ring width–precipitation correlations of

stressed trees confirm that better growth conditions result in higher biomass investments in both below-ground and aboveground wood, and not in preferential investment in aboveground structures.

We hypothesized that drought-stressed trees would have proportionally more root and less shoot mass than reference trees as a response to greater limitation of below-ground resources, and indeed our data supported this hypothesis (Fig. 1). We further hypothesized that stressed trees would allocate more biomass to aboveground wood and less to leaves than reference trees to minimize the risk of hydraulic failure (Sterck et al. 2008; Zweifel and Zeugin 2008; Galle et al. 2010). However, the opposite was true: in the very dry 2004 growing season, stressed trees invested a greater biomass fraction in leaves than reference trees (Fig. 1). Early season growth of leaves (Wardlaw 1990) and twigs (Bréda et al. 2006) is supported by carbohydrate reserves, so current season growth is affected by the previous growing season. The 2003 growing season was extremely warm and dry (Ciais et al. 2005). Severe drought suppresses photosynthesis in *Q. pubescens* and consequent depletion of carbohydrate storage reduces foliage growth in the subsequent growing season in saplings (Galle et al. 2010). Nevertheless, the proportional allocation to leaves in 2004 was greater in stressed trees than in reference trees.

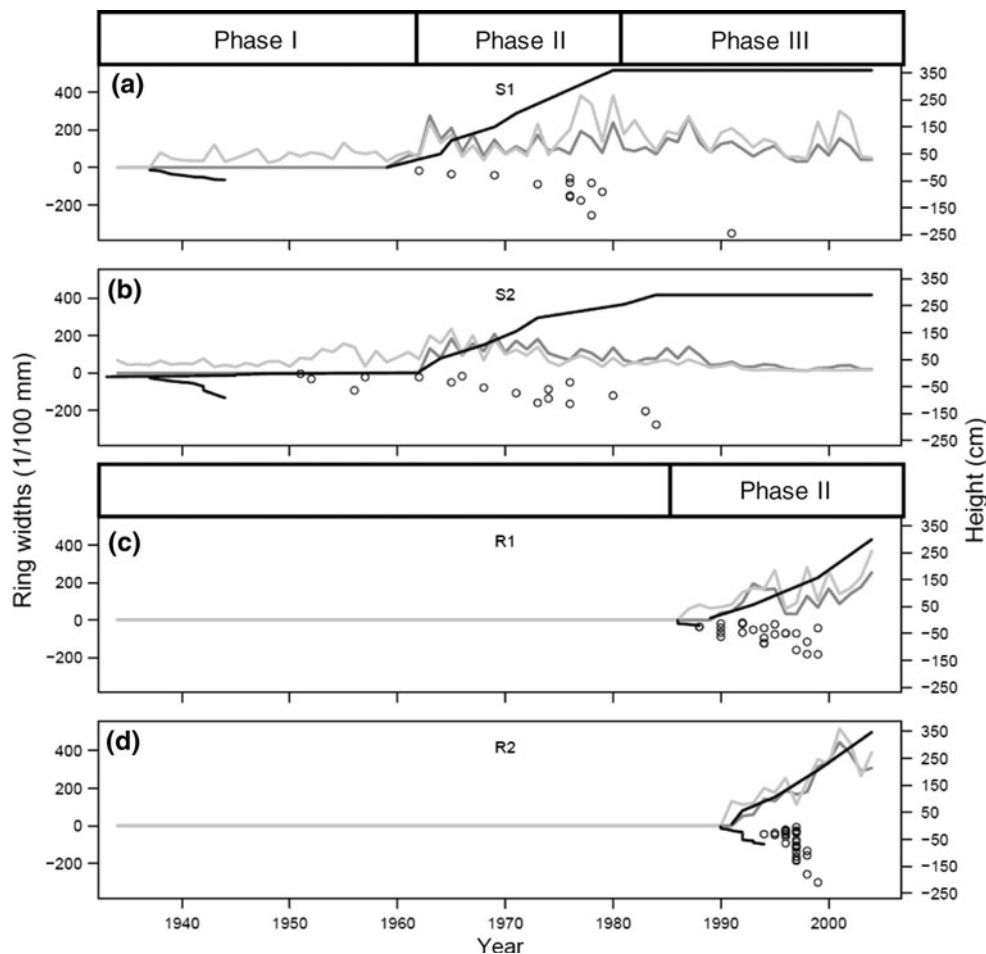


Fig. 3 Annual ring width (light grey lines primary roots, dark grey lines stems), and height (black lines) of stressed (a, b) and reference (c, d) *Q. pubescens* trees. Height in this figure refers to the highest position along the stem at which side branches were present. Actual height could not be determined for every point in time, but using the age of branches at different heights the height growth pattern was reconstructed. Using height of the highest branch means that total tree height is necessarily slightly underestimated. Height growth of stressed oaks ceased 25 years prior to harvest and a clear top shoot

was missing. Hence, the line representing total height is horizontal from the point where the highest branch was recorded. Growth of the primary root is shown as negative height growth. Circles indicate the distance of secondary roots from the soil surface (measured along the root) in the year they first appeared. The tips of excavated roots were all >1 year old, so although no coarse roots developed in recent years, we cannot conclude that root growth had ceased altogether. For the stressed oaks, the three phases of growth (see body text) are indicated

These stressed oaks have lower stomatal (Zweifel et al. 2009) and stem hydraulic conductance (Sterck et al. 2008) and therefore greater water use efficiency (Field et al. 1983) than reference oaks. This might enable stressed trees to invest more in leaves when less water acquisition and transport structures would be required per unit leaf area to replace transpired water. An additional explanation could be that high leaf investments enable stressed trees to enhance carbon gain during short, relatively wet periods in the early growing season. Damesin and Rambal (1995) found that *Q. pubescens* trees cope with summer drought by concentrating photosynthetic production in the less dry spring season. Such a strategy might be at the cost of higher risks of cavitation and low carbon gain during dry periods (Cannell and Dewar 1994; Nardini and Pitt 1999;

Sterck et al. 2008), because *Q. pubescens* is not drought deciduous. Wood anatomical adjustment in response to drought, as observed for *Q. pubescens* trees at this site, does, however, help minimize risk of hydraulic failure even during severe summer drought (Galle et al. 2010).

Our third hypothesis also has to be rejected: we did not find preferential investment below ground during dry years and above ground during wetter years. Cannell and Dewar (1994) suggested that decreased stomatal resistance should result in decreased allocation to water acquisition. Oak trees at the dry site have higher stomatal resistance than at the reference site (Zweifel et al. 2009) and do maintain proportionally more root biomass, but our dendrochronological reconstruction shows that decreased stomatal resistance in wetter years does not result in a decrease in

root growth. Axelsson and Axelsson (1986) also found that although drought (of *P. silvestris* trees) reduced photosynthesis (presumably through increased stomatal resistance) the effects on biomass partitioning were small. Possibly, sub-seasonal dry spells triggered temporary shifts in allocation patterns, but across growing seasons such a pattern did not exist. To better understand the plasticity of biomass allocation and its role in maintenance of functional homeostasis of trees under water stress conditions quantification of seasonal or annual investment of biomass in leaves and fine roots will be necessary (Magnani et al. 2000).

We used stem analysis at the whole-tree level to assess growth and distribution of biomass in *Q. pubescens* trees at two sites with different water availability. Disentangling biotic and abiotic factors from ontogenetic ones remains challenging. Size matching for comparing biomass allocation patterns between trees with different growth rates creates an inherent problem: trees have developed in different time windows characterized by specific conditions, including changes in management practices, or even climate change (e.g. Carnicer et al. 2011). Our study included a limited number of root systems, extracted from one very dry site, so generalizations about the lifetime growth patterns of “dry woodland trees” cannot be made. However, the approach chosen illustrates how mature trees allocated biomass and maintained functional balance in response to multiple stresses, whether biotic or abiotic, during their lives, something that is not easily studied in controlled experiments. Our method further enabled us to show that radial growth in both roots and stems is driven by water availability for *Q. pubescens* trees at the study site, whereas growth of reference trees was less driven by water availability, at least at the annual scale.

We conclude that the growth responses of trees beyond seedling stage are different from those of seedlings, and that this can be analyzed successfully using whole-tree stem analysis. The analysis of sub-seasonal patterns in growth and biomass allocation would, however, require additional techniques.

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